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Host physiological condition regulates parasitic plant performance: *Arceuthobium vaginatum* subsp. *cryptopodum* on *Pinus ponderosa*

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Abstract Much research has focused on effects of plant parasites on host-plant physiology and growth, but little is known about effects of host physiological condition on parasite growth. Using the parasitic dwarf mistletoe *Arceuthobium vaginatum* subsp. *cryptopodum* (Viscaceae) and its host *Pinus ponderosa*, we investigated whether changes in host physiological condition influenced mistletoe shoot development in northern Arizona forests. We conducted two studies in two consecutive years and used forest thinning (i.e., competitive release) to manipulate host physiological condition. We removed dwarf mistletoe shoots in April, before the onset of the growing season, and measured the amount of regrowth in the first season after forest thinning (Study I: $n = 38$ trees; Study II: $n = 35$ trees). Thinning increased tree uptake of water and carbon in both studies, but had no effect on leaf N concentration or $\delta^{13}C$. Mistletoe shoot growth was greater on trees with high uptake of water and carbon in thinned stands than trees with low uptake in unthinned stands. These findings show that increased resource uptake by host trees increases resources to these heterotrophic dwarf mistletoes, and links mistletoe performance to changes in host physiological condition.

Keywords Arizona · Dwarf mistletoe · Forest management · Host-parasite physiology · Photosynthesis · Water relations

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Introduction

Dwarf mistletoes (*Arceuthobium* spp., Viscaceae) are obligate heterotrophic plants that infect numerous conifer species in western North America and around the world (Hawksworth and Weins 1996; Kolb 2002). Species in *Arceuthobium* are host-specific parasites, with most dwarf mistletoes having primary and secondary host species (Hawksworth and Weins 1996). The dwarf mistletoes are similar to the leafy mistletoes of the Loranthaceae and other families because they acquire all of their water and nutrients from their hosts (Fisher 1983; Lamont 1983). However, dwarf mistletoes differ from many other types of mistletoe because they are essentially leafless and are more heterotrophic (Hull and Leonard 1964b; Miller and Tocher 1975; Logan et al. 2002).

Most research on dwarf mistletoes has focused on negative effects of infection on host performance (e.g., Hawksworth and Shaw 1984; Wanner and Tinnin 1986, 1989; Hawksworth and Geils 1990; Tinnin and Knutson 1999; Sala et al. 2001; Godfree et al. 2002; Meinzer et al. 2004), and understanding of their physiological characteristics (e.g., Hull and Leonard 1964a, 1964b; Leonard and Hull 1965; Miller and Tocher 1975; Quarishi et al. 1977; Fisher 1983; Rey et al. 1991; Logan et al. 2002). However, the once dominant view of dwarf mistletoes as detrimental, based on economical impacts on host plant productivity is expanding to include them as keystone-type species that are important to ecosystem food-webs (Mathiasen 1996; Watson 2001; van Ommeren and Whitham 2002; Mooney 2003). For example, forest management in the western U.S. used to emphasize control or sanitation of dwarf mistletoes from conifer stands (Quick 1964; Baranyay and Smith 1972), whereas the value of dwarf mistletoes for animal habitat and structural diversity is increasingly being recognized (Keith 1965; Stevens and Hawksworth 1970; Farentinos 1972; Hawksworth and Geils 1996; Bennetts and Hawksworth 1992; Garnett 2002).

In contrast to the large amount of information on impacts of dwarf mistletoes on their hosts, understanding of factors that regulate the performance of plant parasites such as dwarf mistletoes is sparse (Ayers and Lombardero 2000, Pennings and Callaway 2002). The few studies of this topic have used non-experimental correlative approaches to suggest regulation of mistletoe water use efficiency by the amount of nitrogen (N) contained in the host for partially heterotrophic mistletoes (Schulze and Ehleringer 1984; Schulze et al. 1991), positive relationships between mistletoe abundance and host shoot water potential (Bannister et al. 1999), positive relationships between mistletoe abundance and light intensity in the host canopy (Scharpf 1972; Shaw and Weiss 2000), and linkage between host colonization and chemical composition of host phloem and xylem (Linhart et al. 1994; Snyder et al. 1996). These findings are consistent with the hypothesis that dwarf mistletoe performance is regulated by the physiological condition of the host, analogous to the regulation of the performance of non-parasitic plants by availability of water and mineral nutrients from the soil. In contrast, a descriptive non-experimental study of *Arceuthobium divericatum* on *Pinus edulis* found greater dwarf mistletoe infection in trees in high stress sites compared with low stress sites (Mueller 2004). Experimental tests of the hypothesis that host physiological condition regulates mistletoe performance are needed but are limited to effects of N fertilization of hosts on the physiology of *Phoradendron juniperinum*, which is more autotrophic than the dwarf mistletoes (Marshall et al. 1994). Moreover, few experiments have considered treatments used to improve resource uptake of host trees, such as forest thinning, that are applied widely over forest landscapes (Covington et al. 1997; Latham and Tappeiner 2002; Nyland 2002; Conklin 2003).

We investigated linkages between improved physiological condition of ponderosa pine (*Pinus ponderosa* Laws. var. *scopulorum* Engelm), brought about by forest thinning, and performance of Southwestern dwarf mistletoe (*Arceuthobium vaginatum* [Willd.] Presl subsp. *cryptopodum* [Engelm.] Hawksw. and Weins) by measuring host tree physiological status in thinned and unthinned stands coupled with measurements of mistletoe shoot growth. Much research has shown that forest thinning increases water and carbon uptake of ponderosa pine (Feeney et al. 1998; Kolb et al. 1998; Latham and Tappeiner 2002; McDowell et al. 2003; Skov et al. 2004). We hypothesized that forest thinning would increase resource uptake by host trees, which in turn would increase resources to the dwarf mistletoes and stimulate mistletoe shoot growth.

Methods

Site description

We conducted two similar experiments at different sites in consecutive years (2003, 2004). Stands were approximately 40 ha in size and thinned from below (i.e., most small diameter trees were removed) to simulate tree density and structure found in northern Arizona prior to Euro-American settlement in the late nineteenth century (Covington et al. 1997). Both sites were located near Flagstaff, AZ at elevations exceeding 2,000 m in a climate that is characterized by dry weather in May and June, followed by monsoon thunderstorms between mid-July and mid-September (Sheppard et al. 2002). Over the last 50 years an average of 47% of precipitation has occurred in winter (November–March), 34% during the monsoon thunderstorms (July–September), with the remaining 19% falling in other months [Western Regional Climate Center; http://www.wrcc.dri.edu/index.html]. The sites were located in the ponderosa pine forest-type, which is dominated by ponderosa pine interspersed with junipers (*Juniperus* spp.), Gambel oak (*Quercus gambellii*), and bunch-grasses.

Study I

The 2003 study was located in the Coconino National Forest at an elevation of approximately 2,400 m. Soils on the site were Mollic Eutroboralts derived from mixed igneous parent material (Miller et al. 1995). One half of the study site was assigned a thinning treatment. The two stands (thinned, unthinned) were located next to each other and had the same slope and aspect. In the thinned stand, all competing trees, defined as all trees within a circular perimeter around each subject tree equal to 40× diameter at breast height (DBH), were felled with chainsaws in January 2003; all other thinning was done between May and July 2003 under the auspices of the USDA Forest Service by a logging company. Study trees in unthinned stands for both studies were located more than 20 m from the thinned stand. We measured post-thinning basal area using a random grid design comprising ten 0.1 ha plots spaced 100 m apart in each stand. Tree basal area in the stand before thinning averaged 42.1 m^2/ha; thinning reduced basal area by 41% to 24.7 m^2/ha in the part of the stand assigned the thinning treatment.

We selected trees for physiological measurements by first identifying nineteen trees infected with dwarf mistletoe in the thinned stand. We then paired these trees with trees of similar DBH (mean = 11.6 cm; range = 4–44 cm; $P = 0.50$ t-test between stands) and dwarf mistletoe rating (DMR) (Hawksworth 1977) in the unthinned stand. DMR is a measure of mistletoe infection whereby each third of a tree is evaluated for infection (0, 1, 2) and summed to obtain whole-tree infection on a scale from 0 (uninfected) to 6 (heavily infected) (Hawksworth 1977). Mean DMR of trees in the thinned stand was 4.1 and ranged from 1 to 6; mean DMR of trees in the unthinned stand was 4.6, ranged from 3 to 6, and was similar to the DMR of trees in the thinned stand (t-test $P = 0.26$).

We used forest thinning to reduce inter-tree competition and increase resource availability to trees in the thinned stand. We quantified competition for each tree with the Hegyi (1974) competition index (CI; Lorimer 1983):

$$CI_i = \sum \left(\frac{d_j}{d_i}\right)\left(\frac{1}{D_{ij}}\right)$$

where CI_i is the competition index for the subject tree i, d_j the DBH of the competitor tree j (cm), d_i the DBH of the subject tree i (cm), D_{ij} the distance between the subject i and competitor trees j (m). Competing trees were defined as all trees within a circular perimeter around each subject tree equal to 40× DBH. A previous study showed that trees further away than 40× DBH have little effect on ponderosa pine growth (Sutherland 1989). The calculated CI indicate that competition among trees after thinning was much greater (ANOVA; $P = 0.002$) in the control stand (CI = 2.8, SE = 0.79) than the thinned stand (CI = 0.17, SE = 0.07).

Study II

Study II was performed to test the robustness of results from Study I, and was similar to Study I with the following differences. The 2004 study was in a ponderosa pine stand located in the Northern Arizona University Centennial Forest at an elevation of approximately 2,130 m with no significant slope. Soils on the site were Mollic Eutroboralfs derived from benmorite parent material (Miller et al. 1995). One half of the stand was assigned a thinning treatment. Thinning in September 2003 reduced tree basal area by 57% from 32.8 to 14 m^2/ha. We measured inter-tree competition as described for the 2003 study and found that CI was higher (ANOVA; $P < 0.0001$) for trees in the control stand (CI = 10.7, SE = 2.29) compared to trees in the thinned stand (CI = 0.08, SE = 0.05) after thinning. Eighteen mistletoe-infected ponderosa pines of similar DBH (mean = 9.3 cm; range = 5–28 cm; $P = 0.39$ t-test between stands) and DMR (mean = 3.6; range = 2–6; $P = 0.62$ t-test between stands) were selected for study in each of the thinned and unthinned stands. One tree in the thinned stand died and was removed from the study, making $n = 35$.

Mistletoe removal experiment

Because dwarf mistletoe infections on branches of study trees were mature, we used the amount of regrowth following shoot removal as a measure of resources available from the host tree to the mistletoe. Most storage of carbohydrates and mineral nutrients of *Arceuthobium* has been reported to occur in aerial shoots (Rey et al. 1991), suggesting little resource storage in the endophytic system, and hence a high dependence on resources from the host for aerial shoot growth. We removed dwarf mistletoe shoots from one to three branches per tree, depending on branch availability, in the last week of April in 2003 for Study I (thinned stand mean removed biomass (per tree) = 2.4 g, range = 0.09–9.2 g; unthinned stand mean = 1.7 g, range = 0.30–4.7 g) and in 2004 for Study II (thinned stand mean = 4.8 g, range = 0.46–45.4 g; unthinned stand mean = 4.0 g, range = 1.4–10.6 g), before the onset of the growing season. Branches were selected based on accessibility and presence of mistletoe aerial shoots, and were located approximately 2.3 m above the ground. All removed mistletoe shoot biomass was dried for 72 h at 80°C and weighed. All mistletoe shoots were again removed from the same branches in November of both study years, oven-dried, and weighed. We calculated the percent of mistletoe biomass that regrew from April–November as:

$$\%\ \text{dwarf mistletoe biomass regrowth} = \frac{B_r}{B_o} \times 100$$

where B_r is mistletoe shoot biomass regrowth after removal, and B_o is initial mistletoe shoot biomass removed. Mean mistletoe regrowth was calculated for trees with more than one study branch by averaging over branches.

Host tree physiology

Host physiological status was evaluated by measuring light saturated (PPFD = 1,200 μmol m^2/s) net-photosynthetic rate (P_n), stomatal conductance (g_s), internal CO_2 concentration (C_i), leaf-level N concentration, and leaf $^{13}C/^{12}C$ isotope discrimination ($\delta^{13}C$). We measured P_n, g_s, and C_i of ponderosa pine needles between the hours of 0930 and 1230 using a Li-Cor 6400 portable photosynthesis system (Li-Cor Inc.; Lincoln, NE). We measured one sunlit branch used in the mistletoe removal experiment on each tree in June, August, September, and October 2003 in Study I, and monthly between May and November 2004 in Study II. We measured P_n, g_s, and C_i on 1-year-old needles in May (2004) and June (both years), and on fully developed current-year needles for the remainder of both growing seasons. We coupled gas exchange measurements with measurements of leaf xylem predawn water potential (Ψ_{pre}) using a Scholander-type pressure bomb (PMS Instrument Co.; Corvallis, OR, USA) in all months except August and September 2004, when up to three days separated gas exchange and predawn water potential measurements due to inclement weather conditions. We used projected leaf area measured with AgImage Plus Ver. 1.08 software (Decagon Devices) to calculate P_n and g_s for ponderosa pine and P_n for dwarf mistletoe aerial shoots.

We measured leaf-level N concentration to assess whether differences in carboxylation efficiency existed between trees in the thinned and unthinned stands, as leaf-level N concentration is strongly associated with

rubisco concentration, the primary carboxylating enzyme in C3 plants (Field and Mooney 1986). We measured $\delta^{13}C$ as an index of C_i over the period of needle development (late May–late July). After cessation of current year needle growth at the end of July in both studies we collected a sample of needles, representative of all needles formed during the current season to avoid intra-seasonal bias, from one branch used in the mistletoe removal experiment on each tree for measurement of $\delta^{13}C$ and N concentration. Needle samples were dried for 24 h at 70°C and then ground to a 40-mesh (420 micron) powder using a Wiley Mill (Thomas-Wiley). Samples were analyzed with an Elemental Analyzer-Continuous Flow Isotope Ratio Mass Spectrometer (Finnigan Delta Advantage) at the Colorado Plateau Stable Isotope Laboratory (2005) at Northern Arizona University, Flagstaff, Arizona (http://www4.nau.edu/cpsil/).

Light response curves

We measured photosynthetic light response curves on one branch infected with dwarf mistletoe from each of eight trees, and on the mistletoe shoots growing on those branches. Measurements were made in the first week of September 2004 between the hours of 0800 and 1200 in the unthinned stand at the Study II site, on different but similar-sized trees to those used for the mistletoe regrowth measurements. We measured P_n using a Li-Cor 6400 portable photosynthesis system at the following levels of PPFD (Photosynthetic Photon Flux Density: $\mu mol/m^2/s^1$): 50, 100, 300, 400, 600, 700, 800, 1,000, and 1,200. Leaves and mistletoe shoots acclimated to each level of PPFD for approximately two minutes prior to measurement. Chamber CO_2 concentration was maintained at 365 ppm, chamber humidity was maintained within 10% of ambient, and leaf temperature was maintained at 25°C during measurement. We first measured light response curves from pine needles attached to the tree. The branch supporting these needles was excised from the tree, the cut end was immediately placed under water and then re-cut to remove xylem embolisms, and the cut end remained submerged throughout the light response measurements for mistletoe. Measuring light response curves of dwarf mistletoe shoots on cut branches helped prevent breakage of fragile dwarf mistletoe shoots. Additional measurements of the response of mistletoe P_n to PPFD were made in early June 2005 to better understand carbon uptake of mistletoe at low light levels. These measurements were made on five mistletoe plants growing on five different trees at the Study II site using identical techniques to those used in June 2004, except that we focused only on low levels of PPFD (0, 75, 200, 400 $\mu mol/m^2/s^1$) and included a measurement of dark respiration.

Data analysis

Analysis of the data from Study I with repeated measures MANOVA revealed that the original pairing design based on similar tree DBH and DMR had no effect on Ψ_{pre} ($P = 0.20$), P_n ($P = 0.69$), g_s ($P = 0.33$), or C_i ($P = 0.49$). Consequently, all tree physiological data from Study I and II were analyzed separately without pairing by tree size or DMR with one-way ANOVA or repeated measures MANOVA for measurements repeated over different dates (Study I: $n = 38$; Study II: $n = 35$). Due to a limited number of repeated measurements of tree physiological characteristics (Ψ_{pre}, P_n, g_s, C_i) our multivariate tests were transformed into univariate tests (Huynh and Feldt 1970; SAS Institute 2002). Effects of date and treatment × date interactions on measurements were evaluated using epsilon-adjusted tests. When significant treatment × date interactions occurred data were analyzed by date using ANOVA with a Bonferroni adjustment for comparisons over multiple dates. If the sphericity chi-square test was significant we evaluated date and treatment interactions using the Geisser and Greenhouse adjusted-univariate test. If the sphericity chi-square test was not significant we evaluated interactions using unadjusted-univariate F tests (SAS Institute 2002). We compared leaf-level N concentration and $\delta^{13}C$ between thinned and unthinned stand trees using ANOVA. We pooled mistletoe biomass regrowth data across studies and analyzed these data using ANOVA with study, treatment, and treatment × study as factors and with tree DBH as a covariate.

Results

Host tree physiological response to thinning

Study I

Precipitation during the 2003 growing season was 22% below average for northern Arizona (Western Regional Climate Center). Host-tree Ψ_{pre} was significantly higher in the thinned stand across time ($P = 0.006$), though there was substantial variation throughout the growing season (Fig. 1a). Trees in both thinned and unthinned stands were most stressed in July, as indicated by the lowest Ψ_{pre}, and least stressed in August during the monsoon rains (Fig. 1a). Rains in late August and early September saturated soils so that mean Ψ_{pre} in the two stands was identical in mid-September. Lack of precipitation between cessation of the rainy period in mid-September to October lowered Ψ_{pre} in both stands (Fig. 1a).

Results for P_n, g_s, and C_i indicate consistently higher carbon uptake by trees in the thinned stand compared with trees in the unthinned stand. Stomatal conductance ($P < 0.0001$; Fig. 1b) and C_i ($P = 0.06$; Fig. 1c) were higher for trees in the thinned stand. Differences in P_n between trees in thinned and unthinned stands depended on measurement date (treatment × date interaction: $P = 0.03$; Fig. 1d). Bonferonni adjusted ANOVA ($P \leq 0.0125$ level) comparisons show significantly higher P_n for trees in the thinned stand in August ($P = 0.01$),

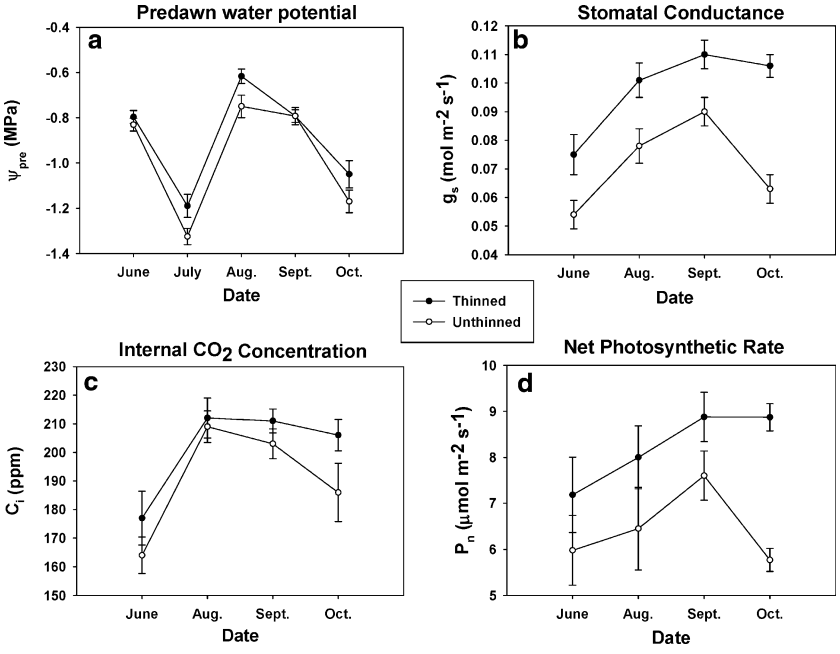

Fig. 1 Host-tree physiological characteristics for Study I ($n = 38$) in thinned and unthinned stands. Ponderosa pine trees in the thinned stand had higher leaf-xylem predawn water potential (Ψ_{pre}) (**a**; $P = 0.006$), stomatal conductance (g_s) (**b**; $P < 0.0001$), internal CO_2 concentration (C_i) (**c**; $P = 0.06$) and net photosynthetic rate (P_n) (**d**) than trees in the unthinned stand. There was a significant treatment x date interaction for P_n ($P = 0.03$). Bonferonni-adjusted analyses by date showed P_n was higher for trees in the thinned stand than the unthinned stand in August, September, and October, but not in June P_n ($P = 0.02$) (**d**). *Bars* indicate one SE

September ($P = 0.001$), and October ($P < 0.0001$), but not in June ($P = 0.02$). Leaf N concentration was similar for trees in both stands ($P = 0.55$; mean thinned = 1.21%, SE = 0.07; mean unthinned = 1.26%, SE = 0.06), suggesting that higher P_n in the thinned stand was due to increased g_s and not greater carboxylation efficiency. Leaf-level $\delta^{13}C$ for needles formed in 2003 was similar ($P = 0.73$) in both stands (mean thinned = −26.46‰, SE = 0.21; mean unthinned = −26.36‰, SE = 0.18).

Study II

Precipitation during the 2004 growing season was 16% below average for northern Arizona (Western Regional Climate Center). Trees were most water stressed in July, as indicated by low Ψ_{pre}, and least water stressed in September (Fig. 2a). Host-tree Ψ_{pre} was higher in the thinned stand than the unthinned stand across time ($P < 0.0001$), but differences in Ψ_{pre} between stands depended on measurement date (treatment × date interaction $P < 0.0001$). Subsequent analyses of each individual month using Bonferonni adjusted ANOVA ($P \leq 0.007$ level) showed that Ψ_{pre} was significantly higher for trees in the thinned versus the unthinned stand between June and October, but not in May ($P = 0.41$) or November ($P = 0.76$) (Fig. 2a). We attribute this similarity in Ψ_{pre} between stands in May and November to wet soil conditions across the study site. Overall, trees in the thinned stand showed significantly less water stress compared to trees in the unthinned stand, with a more striking difference between stands in Study II than Study I (Figs. 1a, 2a).

We measured host-tree physiological indicators across more of the growing season in Study II than Study I, and found more variability among months. Differences in g_s between thinned and unthinned stands depended on measurement date (treatment × date interaction $P = 0.002$; Fig. 2b). Bonferonni adjusted ANOVA ($P \leq 0.007$ level) comparisons showed g_s was higher for trees in the thinned stand compared with the unthinned stand from May through September, but not in October ($P = 0.56$) and November ($P = 0.18$), a change we attribute to wet soil conditions and low night time temperatures in both stands in October and November. Differences in C_i between stands also depended on measurement date (treatment × date interaction $P = 0.001$; Fig. 2c). Analyses of individual months ($P \leq 0.007$ level) showed higher C_i in trees in the thinned stand than the unthinned stand in May ($P = 0.003$), June ($P < 0.0001$), and September ($P < 0.0001$) with generally, but not significantly, higher C_i in most other months (Fig. 2c). Differences in P_n also depended on measurement date (treatment × date interaction $P < 0.0001$); P_n was higher ($P \leq 0.007$ level) in the thinned stand until October ($P = 0.46$) and November ($P = 0.14$) (Fig. 2d). Leaf N concentration was similar between stands ($P = 0.17$; mean thinned: 1.12%, SE = 0.04; mean control: 1.19%, SE = 0.03), suggesting similar carboxylation efficiency. We also found similar leaf-level $\delta^{13}C$ ($P = 0.79$) for thinned and unthinned stands (mean thinned = −24.79‰, SE = 0.16; mean control = −24.84‰, SE = 0.12) for needles formed in 2004.

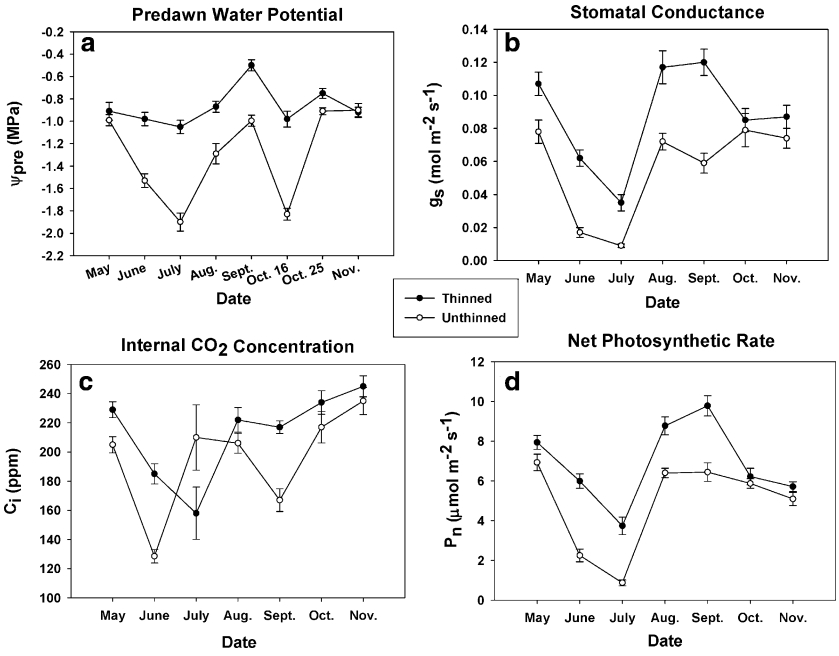

Fig. 2 Host-tree physiological characteristics for Study II ($n = 35$) in thinned and unthinned stands. Ponderosa pine trees in the thinned stand had higher leaf-xylem predawn water potential (Ψ_{pre}) (**a**), stomatal conductance (g_s) (**b**), generally higher internal CO_2 concentration (C_i) (Fig. 2C), and higher net photosynthetic rate (P_n) (**d**) than trees in the unthinned stand. There was a significant treatment x date interaction for Ψ_{pre} ($P < 0.0001$; **a**). Bonferroni adjusted ANOVA ($P \leq 0.0063$) showed trees in the thinned stands had higher Ψ_{pre} in all months except May and November. There was a significant treatment × date interaction for g_s ($P = 0.002$; **b**). Bonferroni adjusted ANOVA ($P \leq 0.007$) showed trees in the thinned stand had higher g_s in all months except October and November (**b**). There was a significant treatment × date interaction for C_i ($P = 0.001$; **c**). Bonferroni adjusted ANOVA showed trees in the thinned stand had higher C_i in May, June, and September ($P \leq 0.007$; **c**), but not in other months. C_i was higher in the unthinned stand in July, consistent with a severe water stress effect on carboxylation potential. There was a significant treatment × date interaction for P_n ($P < 0.0001$; **d**). Bonferonni adjusted ANOVA ($P \leq 0.007$) showed trees in the thinned stand had higher P_n in all months except October ($P = 0.46$) and November ($P = 0.14$). *Bars* indicate one SE

Dwarf mistletoe shoot growth

Host-tree DBH was a significant covariate with mistletoe shoot regrowth ($P = 0.008$), thus we present regrowth data using least square means adjusted to the same DBH (Fig. 3). In contrast, host-tree DMR was not significantly correlated with mistletoe shoot regrowth ($P = 0.26$). Dwarf mistletoe shoot regrowth was greater in the thinned stand than in the unthinned stand in both studies (Fig. 3; $P = 0.05$; $n = 73$). Regrowth was similar between studies ($P = 0.54$) and differences in regrowth between thinned and unthinned stands were similar between studies (treatment × study interaction $P = 0.57$).

Light response curves

We found evidence for limited photoautotrophic capacity in *A. vaginatum* subsp. *cryptopodum*. In September 2004, mistletoe shoots had consistently negative P_n at all PPFD levels (Fig. 4). The only significant change in mistletoe P_n among PPFD levels ranging from 50 to 1,200 μmol/m^2/s^1 in September 2004 was a small decrease between 400 and 1,200 PPFD (*t*-test $P < 0.01$; Fig. 4). In contrast to mistletoe, ponderosa pine needles had consistently positive P_n at all PPFD levels in September 2004 (Fig. 4), with light saturation occurring at approximately 600 μmol/m^2/s^1.

Mistletoe P_n measured in June 2005 was again well below zero at all PPFD levels (Fig. 4). Increasing P_n with increasing PPFD between 0 and 400 μmol/m^2/s^1 (*t*-test $P = 0.007$) suggests that mistletoe carbon balance in June included a small amount of CO_2 assimilation from the atmosphere at low PPFD. For example, the mean P_n of −4.2 μmol/m^2/s^1 at PPFD = 400 μmol/m^2/s^1 consisted of 1.2 μmol/m^2/s^1 of gross photosynthesis that offset a dark respiration rate of 5.4 μmol m^2/s^1 (Fig. 4). An additional finding from the June 2005 measurements was large temporal variation in CO_2 exchange of mistletoe shoots. Mistletoe P_n was more negative in June 2005 than in September 2004 (Fig. 4) at similar PPFD levels (e.g., *t*-test $P = 0.008$ for PPFD = 400 μmol/m^2/s^1).

Discussion

Thinning increased host-tree Ψ_{pre}, and hence water uptake, in both studies (Figs. 1a, 2a). Increases in Ψ_{pre} in both studies were consistent with increases in thinned and thinned and burned ponderosa pine stands compared with unthinned stands on other study sites in northern Arizona (Feeney et al. 1998; Kolb et al. 1998; Skov et al. 2004). Differences in Ψ_{pre} between thinned and unthinned stands were more pronounced in Study II than Study I (Figs. 1a, 2a), probably due to lower tree basal area after thinning and greater competitive release

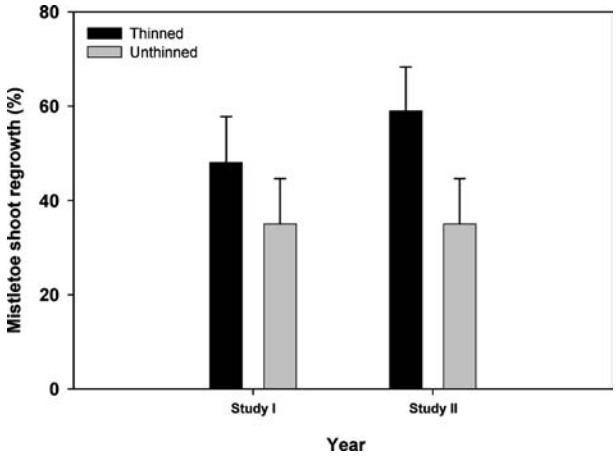

Fig. 3 Mistletoe shoot regrowth was higher on trees in the thinned stand than the unthinned stand in both studies ($P = 0.05$; $n = 73$). Mistletoe regrowth did not differ between studies ($P = 0.54$) and differences between thinned and unthinned stands were consistent between studies (treatment × study interaction $P = 0.57$). Means represent least square means with tree DBH as a covariate ($P = 0.008$). Bars represent one SE

in Study II. Peak water stress in unthinned stands was more severe in Study II (minimum $\Psi_{pre} = -1.9$ MPa) than Study I (minimum $\Psi_{pre} = -1.3$ MPa). The lowest Ψ_{pre} reported for ponderosa pine in northern Arizona is about −2.0 MPa (Simonin et al. 2005, Skov et al. 2004). Thus, water stress in the Study II unthinned stand was severe for this region. Consistent with our results, the lowest Ψ_{pre} in northern Arizona usually occur in early July, after dry spring weather and before the onset of monsoon rains (Kolb and Stone 2000).

Increased water availability in thinned stands increased tree carbon uptake. Tree light-saturated P_n was higher in trees in thinned than unthinned stands throughout most of both studies (Figs. 1d, 2d). Higher water availability likely contributed to higher g_s in trees in the thinned stand (Figs. 1b, 2b), which increased P_n as leaf-level N concentration was similar between stands in both studies, implying similar carboxylation efficiency. Leaf g_s has been reported to be strongly correlated with P_n in other studies of ponderosa pine, and for other plant species (Wong et al. 1979; Feeney et al. 1998; Skov et al. 2004). The higher C_i measured in trees in the thinned stand in most months further supports higher CO_2 availability as the dominant mechanism of higher P_n in the thinned compared with the unthinned stand (Figs. 1c, 2c). C_i was higher in the unthinned stand compared with the thinned stand only in July of Study II, probably due to a limitation on carboxylation potential from severe water stress in the unthinned stand, as mid-day light-saturated P_n was close to zero in this stand in July. The only dates in both studies when leaf gas exchange was similar between thinned and unthinned stands were in October and November of Study II when Ψ_{pre} was high (e.g., low water stress) and similar for the thinned and unthinned stand (Fig. 2). Our findings are consistent with previous research that effects of thinning on P_n and g_s of ponderosa pine are greatest when Ψ_{pre} is lowest (Feeney et al. 1998; Kolb et al. 1998; Skov et al. 2004).

$\delta^{13}C$, a time-integrated measurement of the ratio between C_i and ambient CO_2 concentration and hence the ratio between P_n and g_s (Farquhar et al. 1989), was not affected by thinning in either year. Similar findings have been reported by other studies of ponderosa pine in northern Arizona, even when thinning increased P_n and g_s (Skov et al. 2004; Wallin et al. 2004). Significant increases in ponderosa pine leaf $\delta^{13}C$ in northern Arizona have been reported only during extreme droughts that dramatically reduce g_s (Adams and Kolb 2004; Wallin et al. 2004). Similar leaf $\delta^{13}C$ in thinned and unthinned stands may have been caused by increased soil respiration in the thinned stand (Kaye and Hart 1998) resulting in higher atmospheric $^{13}CO_2$ concentration in the lower canopy layer where our leaf samples were collected (Brooks et al. 1997; Buchmann et al. 1997; Flanagan and Ehleringer 1998; Fessenden and Ehleringer 2003), or an effect of irradiance on leaf $\delta^{13}C$ (Waring and Silvester 1994), as thinning increased irradiance on the lower crown branches used in our study. Another explanation supported by our results in Study I is that thinning increased P_n and g_s similarly so that C_i did not change enough during the period of needle development to influence $\delta^{13}C$ of the whole leaf tissue.

Our light response curves show that Southwestern dwarf mistletoe provides for little of its carbohydrate needs by direct photosynthesis, and has large seasonal changes in CO_2 exchange (Fig. 4). Release of CO_2 from mistletoe respiration was much greater than uptake from photosynthesis over a wide range of PPFD levels, resulting in large negative values of P_n. Mistletoe dark respiration rate was 19 to 5 fold greater than gross photosynthesis at low to moderate PPFD (75–400 μmol/m^2/s^1) in June measurements. Photoinhibition of mistletoe photosynthesis by high PPFD is suggested by higher P_n at 400 PPFD than at 1,200 PPFD in September. More negative P_n of mistletoe in June compared with September suggest considerable seasonal variation in respiration driven by the phenology of mistletoe growth or reproduction. In contrast to the domination of mistletoe shoot carbon balance by respiration, P_n of ponderosa pine was positive at all light levels (Fig. 4), with a light saturation point of 600–800 μmol/m^2/s^1 PPFD similar to other reports for this species (Kolb and Robberecht 1996; Bond et al. 1999).

Increased uptake of water and carbon by host ponderosa pine trees, caused by forest thinning, stimulated dwarf mistletoe shoot growth. Thinning increased mistletoe shoot growth by an average of 35% (Fig. 3). The interface between the xylem of the dwarf mistletoe endophytic system and host xylem and phloem regulates mistletoe acquisition of resources, as considerable resistance to the movement of solute from host to mistletoe occurs at this interface (Srivastava and Esau 1961; Alosi and Calvin 1985; Davidson et al. 1989). Despite this resistance, supply of growth-limiting resources from

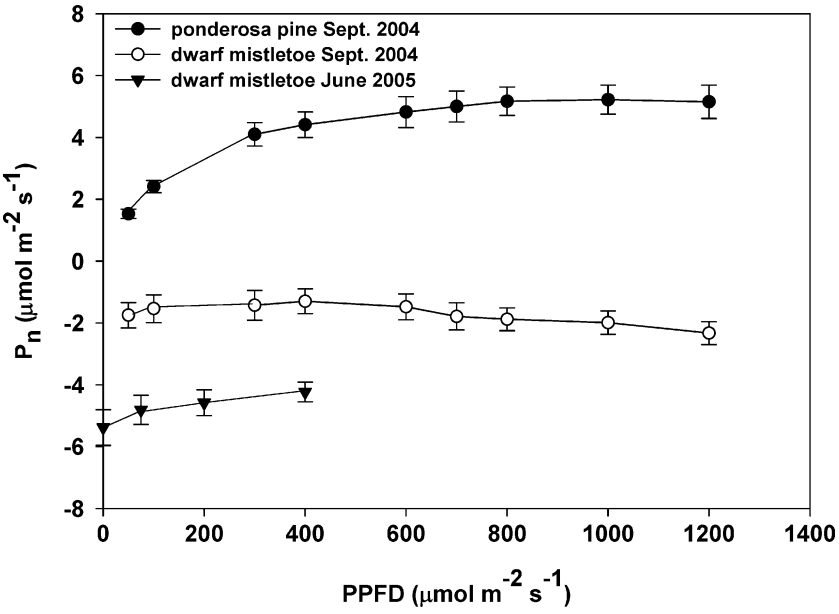

Fig. 4 Net photosynthetic rate (P_n) of ponderosa pine in September 2004 increased in response to increasing photosynthetic photon flux density (PPFD) to a saturation point of about 600 μmol/m^2/s^1. In contrast, P_n of dwarf mistletoe was consistently negative in September 2004 and June 2005, showed little response to changes in PPFD, and was dominated by dark respiration (June curve, PPFD = 0). *Bars* represent one SE

host xylem and phloem to mistletoe xylem apparently increased in response to thinning. The identity of these resources from the host is not clear in our study but probably includes carbon-containing compounds such as cyclitols, amino acids, organic acids, and cytokinins that are known to be utilized by mistletoes from the host (Stewart and Press 1990; Kolb 2002).

One possible confounding factor in elucidating the mechanism behind increased dwarf mistletoe growth in the thinned stands is mistletoe carbohydrate storage prior to thinning. Carbohydrate storage in the dwarf mistletoe endophytic system before thinning could reduce dependence of mistletoe on resources from the host tree supplied after thinning. Early studies suggested that carbohydrate acquired by dwarf mistletoes from host xylem sap accumulated primarily in the endophytic system (Rediske and Shea 1961; Hull and Leonard 1964b). However, more recent evidence from *A. oxycedri* indicated accumulation of most compounds, including carbohydrates, in the aerial shoots of dwarf mistletoe with little accumulation in the endophytic system (Rey et al. 1991). We attempted to eliminate possible effects of mistletoe carbohydrate storage on dwarf mistletoe growth by removing dwarf mistletoe aerial shoots and measuring regrowth from the endophytic system, and by using trees of similar size and DMR and using tree DBH as a covariate in analysis of mistletoe regrowth. This experimental approach clearly showed greater dwarf mistletoe growth on trees in thinned compared with unthinned stands.

Another possible explanation for increased mistletoe shoot growth in the thinned stands is a difference in temperature between thinned and unthinned stands, as tree removal could alter microclimate. The stimulation of mistletoe growth in the thinned stand may have occurred because of warmer temperatures that increased rates of synthesis and expansion of cells of dwarf mistletoe aerial shoots. However, this explanation is unlikely considering the fact that restoration thinning projects similar to those in our study have had little effect on air temperature within a stand (Meyer et al. 2001). It is also possible that mistletoes grew more in the thinned than the unthinned stands because thinning increased tissue water potential of both mistletoe and its host, and thus reduced constraints on mistletoe growth from water stress.

Our findings show that dwarf mistletoes exhibit substantial plasticity in short-term growth which is linked to host physiological condition and resource uptake. We found that increases in water availability and carbon uptake by host trees stimulated mistletoe growth in the lower portion of the tree canopy. Our findings are limited to the lower portion of the canopy as we did not measure mistletoe growth in the mid- and upper-levels of tree canopies. However, our results are similar to a report from New Mexico for the same species used in our study that stand thinning increased dwarf mistletoe infection over the entire canopy of individual trees compared with an unthinned stand (Conklin 2003). The effects of thinning on resource availability to host trees are probably greatest in the first year or two after thinning, as dominance and resource use by herbaceous species and other understory plants increases in subsequent years (Covington et al. 1997; Moore et al. 2005). Long-term effects of changes in host-tree physiological condition by thinning on dwarf mistletoe growth and reproduction are unknown. Increased resources immediately after thinning may stimulate growth of the

mistletoe endophytic system in the short term and increase resource acquisition from host trees in the future. Increased competition with understory plants and remaining trees several years after thinning could diminish resources available to host trees and mistletoes for future growth. Or, tree height growth and crown expansion may be stimulated by thinning more than dwarf mistletoe expansion, resulting in a decrease in long-term tree- and stand-level infection (e.g., Roth and Barrett 1985).

Our finding of increased parasitic plant growth on more vigorous host trees shown by an experiment approach is contrary to a report of greater occurrence of *A. divericatum* on *P. edulis* growing on high stress compared with low stress sites in Arizona shown using a descriptive, non-experimental approach (Mueller 2004). These seemingly contradictory results may be due to differences in the measured mistletoe responses. Greater mistletoe occurrence in a stand implies greater mistletoe establishment and survival, which is different than greater mistletoe growth per branch, the variable we measured. Consistent with our results, biomass of *Melampyrum pretense*, a root parasite, increased on host *Pinus sylvestris* trees grown with ectomycorrhizal fungi that increase tree nutrient uptake (Allen 1991) compared with trees grown without ectomycorrhizae (Salonen et al. 2000). Similarly, growth of *Rhinanthus minor*, a hemiparasitic plant, was greater when its host, *Lolium perenne*, was colonized with arbuscular mycorrhizal fungi (Davies and Graves 1998). These parallel findings suggest that growth of many parasitic plants may be linked to changes in host physiological condition induced by a variety of factors that affect host resource uptake such as competition and mycorrhizae.

In conclusion, growth of the parasitic plant dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum*) is responsive to the physiological condition of the host tree (*P. ponderosa*) similar to the stimulation of growth of a non-parasitic plant by an increase in the supply of a limiting soil resource. The linkage between host-tree physiological condition and dwarf mistletoe performance in our study suggests that changes in resource uptake of host trees by anthropogenic activities (e.g., forest management, air pollution) or by more natural disturbances (e.g., wildfire, insect outbreaks) may have secondary effects on obligate parasitic plants which may ripple through the ecosystem given the keystone status of mistletoes in many forests and woodlands (Watson 2001).

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